Abstract.—The lack of age and growth estimates and population parameters for the amberjack family prompted our study to describe otolith structure and determine size-at-age and growth rates of greater amberjack (Seriola dumerili) from the north-central Gulf of Mexico.

Greater amberjack age and growth was described from a combination of external ridges and internal annuli in sectioned sagittal otoliths. A mark-recapture study using tetracycline was consistent with a single annulus being formed each year in two- and threeyear-old amberjack. Tag-recapture data from the Gulf of Mexico and South Atlantic Cooperative Gamefish Tagging Program also confirmed that a single annulus increment was formed each year. Ages for 597 specimens ranged from young-of-the-year to 15 years, and all fish over 9 years were female. Sagittal weight provided a reliable estimation of fork length with a relationship of $FL = 151 (1 - e^{(-0.04(SW+1.6))})$: a negative exponential equation in the form of the von Bertalanffy equation. The fit of the negative exponential in this application provides evidence of the disassociation between otolith growth and fish growth as fish age. The von Bertalanffy growth curve equation, $L_t = 138.9 (1 - e^{-0.25(t+0.79)}),$ compared favorably with previous published values. Monthly changes in size and availability indicate a Gulf-wide migration of this moderately long-lived pelagic predator.

Age distribution and growth of greater amberjack, *Seriola dumerili*, from the north-central Gulf of Mexico*

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The greater amberjack, *Seriola dumerili*, is a pelagic reef species ranging along the American coasts from Nova Scotia to Brazil and occurring throughout the Atlantic, Pacific, and Indian oceans, as well as the Mediterranean Sea (Mather, 1958; Burch, 1979; Shipp, 1988). It is the largest member of the family Carangidae (Hoese and Moore, 1977).

Commercial landings of amberjack (all species) have increased markedly over the past twenty years. Landings in the Gulf of Mexico peaked in 1988 reaching 2.7 million pounds, with a dockside value over 1.6 million dollars, but have since declined to less than one million pounds in 1995–96. Recreational catch statistics are incomplete but are suspected to have equalled or surpassed the commercial catch, raising concern over the status of the Atlantic stock in the late 1970s (Berry and Burch, 1979). Despite their popularity as a recreational and commercial quarry, little is known about the life histories of amberjacks (Shipp, 1988).

Of particular concern to stockassessment scientists is the lack of age and growth estimates and population parameters for the amberjack family (Burch, 1979; Humphreys, 1986). Burch (1979), using scales, aged greater amberjack from the western Atlantic to 10 years for females and to eight years for males. Females were significantly longer than males beyond age four. Humphreys (1986) reported von Bertalanffy growth parameters for Hawaiian greater amberjack but did not elaborate on how the fish were aged or how many fish were contained in the data set.

The purpose of this study was to collect and describe greater amberjack otoliths, assess their utility in age estimation, and determine the size-at-age and growth rates of greater amberjack from the north-central Gulf of Mexico.

Materials and methods

Sampling

Greater amberjack (*n*=840) were collected off the Louisiana coast from April 1989 to June 1992. Sources of samples included a commercial processor plant (*n*=18), charterboats (*n*=352), saltwater fishing tournaments (*n*=215), spearfishing tournaments (*n*=159), recreational catches (*n*=48), and hook-

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and-line catches from an offshore gas production platform (n=48). In general sampling was not systematic; we examined all fish available.

Morphometric measurements and otoliths were collected. Fish were measured by using fork and total lengths (FL and TL) in mm and weighed by using total and gutted weights in g. Both sagittae were removed and stored in 95% ethanol for later examination. Lapilli, asterisci, and dorsal spines were removed from several fish to evaluate their usefulness for age estimation. Otoliths were cleaned of organic tissue by rinsing in a 50% hypochlorite solution (Clorox), air dried, weighed to the nearest 0.1 mg with a Sartorius model 1801 microbalance, and stored dry (Wilson et al.,1991).

Age estimates were made by using techniques similar to those of Wilson et al. (1991) for billfish. Whole otoliths were sputter coated with a mixture of gold and palladium and viewed with reflected light under a dissecting microscope for description of external morphology. These samples were also viewed with a Cambridge Stereoscan 150 scanning electron microscope (SEM) to obtain detailed photographs at magnifications ranging from 20 to 650×.

Sagittae were embedded in epoxy resin (Spurr, Embed 812, or Araldite GY 502) and sectioned with a Buehler Isomet low-speed saw to yield a thin (about 1-mm) transverse section containing the core (Beckman, 1989). Transverse sections were ground with various grades (300-2000 grit) of wet and dry sandpaper until the core was at the surface, then polished with 0.3 μm alumina polish. Thin sections were mounted on glass slides with a clear thermoplastic cement (Crystalbond 509) and viewed under transmitted light with an Olympus BH-2 compound microscope at 50–250× magnification. Age estimates from sectioned sagittae were made by combining counts of translucent and opaque zones and other growth features viewed under transmitted light and counts of associated ridges on the ventral and medioventral portions of the rostrum as determined in billfish species (Wilson and Dean, 1983; Prince et al., 1986; Wilson et al., 1991).

Validation and verification of our age estimation technique were attempted by using several techniques. Validation of annulus formation using marginal increment analysis proved futile owing to our inability to determine the condition of the otolith edge. Therefore we pursued additional techniques that would corroborate our age estimates. A markrecapture study was carried out from a gas production platform (Mobil USA, West Cameron block 352) located in the Gulf of Mexico 50 miles south of Cameron, Louisiana. Greater amberjack (n=48) were captured by hook and line, measured as described

above, tagged at the base of the dorsal fin with a Hallprint dart tag, injected with oxytetracycline hydrochloride (Agrimycin-100) at a rate of 20–40 mg/kg fish weight, and released. Tagged greater amberjack (6) were recaptured with hook and line or by spear fishermen at the release site and sampled as described above. Sectioned sagittae were viewed under ultraviolet light (405–435 nm wavelength) at $50-250\times$ magnification for detection of the tetracycline mark. Attempts made to compare age estimates from sagittal otoliths with dorsal and anal spines and vertebrae were not successful. To determine reproducibility of age estimates, sagittae were aged independently by two readers. Reproducibility of age estimates was compared by using the coefficient of variation (CV) and index of precision (D) (Chang, 1982).

Tag-recapture data for the Gulf of Mexico and South Atlantic (*n*=711) were obtained from the Cooperative Gamefish Tagging Program (CGTP). Fish that had been at large for at least 365 days after tagging and that showed positive growth were used. Twenty-five specimens met these criteria. Following the method of Labelle et al. (1993), we used the von Bertalanffy growth curve parameters to predict changes in length from the tag recapture data to verify our age estimates. Like Labelle et al. (1993) we employed Fabens' (1965) length increment model to predict length at recapture:

$$Ir_i = I_i + (L_{\infty} - I_i)(1 - e_i^{-k\Delta t}),$$

where l_i = length at release of individual i;

 Δt_i = time of liberty of individual *i*;

 lr_i = estimated length-at-recapture of indi-

vidual *i*; and

 L_{∞} and k = von Bertalanffy parameters estimated from otolith ages.

Predicted recapture lengths were then compared with observed recapture lengths. As Labelle et al. (1993) pointed out, this procedure is not statistically rigorous but is useful for comparative purposes.

An analysis of variance (ANOVA) was used to test for sex-related differences in mean fork length, mean gutted weight, mean sagittal weight, and mean age among sources and within age class. Analysis of covariance (ANCOVA) was used to test for differences in the relations (fork length [L] versus total weight [Wt], fork length versus sagittal weight [SW], age versus sagittal weight) between sexes (Cerrato, 1990; Kimura, 1980). Statistical inferences were made with a significance level of α =0.05. The relationship between fork length and otolith weight was modeled with a negative exponential (von Bertalanffy) because it provided the best fit (highest r^2).

The von Bertalanffy model $L_t = L_{\infty}(1 - e^{-k(t-t_0)})$ was also used to describe the relation between length and age. Relative ages were assigned to fish by using a birth date of 1 April based on trends in gonadosomatic indices and the regression of sagittal weight on month of capture for young-of-the-year fish. Von Bertalanffy growth parameter estimates for males and females were compared by using a likelihood ratio test at $\alpha = 0.05$ (χ^2 statistic) (Cerrato, 1990; Kimura, 1980).

Results

Length and weight

Greater amberjack ranged from 167 to 1441 mm (FL); females ranged from 374 to 1441 mm (\bar{x} =879 mm), and males ranged from 387 to 1203 mm (\bar{x} =854 mm). Females represented 72% of the fish over 1 m in fork length. There was no significant difference in mean fork length between males and females. Females ranged from 0.82 to 42.5 kg (\bar{x} =11.33) and males ranged from 0.85 to 28.8 kg (\bar{x} =9.90). Mean gutted weight (GW) of females was significantly greater than that of males (ANOVA P>F= 0.03) and females represented 78% of the fish over 20 kg gutted weight. Regressions for TL versus FL and TW versus GW were

Monthly mean fork length and sex ratio from charterboat catches were compared because this was the only year-round source of greater amberjack (Table 1). Charterboats fishing Gulf of Mexico waters off the Louisiana coast caught larger greater amberjack during the summer months (from May to September) and smaller greater amberjack during winter months (from November to February). Sex ratios ranged from 0.4:1 to 4.5:1 (\bar{x} =2.49) (Table 1), and there was a relatively greater abundance of females each month except September.

The relation between fork length (cm) and gutted weight (kg) was best described by a power function. The slopes of the regression lines for males and females were significantly different. The equations explaining these relations were

All samples: $W=4.2\times10^{-5}~L^{2.83}~(r^2=0.99,~n=862)$

Table 1

Monthly mean fork length (mm) and sex ratio of charterboatcaught greater amberjack from the northern Gulf of Mexico ranked by decreasing mean fork length.

	Mean fork length (mm)		Sex ratio female:male
Month		n	
May	771.1	70	2.0
Jul	702.7	11	1.6
Jun	651.0	21	2.7
Sep	613.2	14	0.9
Mar	566.9	75	2.3
Apr	560.4	43	3.5
Nov	482.6	38	2.0
Oct	420.8	59	2.0
Feb	408.4	9	5.0
Dec	383.0	9	0.0
Jan	351.5	2	0.0

Females: $W = 3.25 \times 10^{-5} L^{2.87}$ ($r^2 = 0.98$, n = 324) Males: $W = 1.75 \times 10^{-5} L^{2.96}$ ($r^2 = 0.98$, n = 184) Sex unknown: $W = 7.62 \times 10^{-5} L^{2.87}$ ($r^2 = 0.98$, n = 354)

Otolith structure

Greater amberjack sagittae are small, thin, fragile, and elongate in the anterior direction and bluntly crenelate at the posterior end. The medial surface is convex and has a deep, prominent sulcus. The anterior portion of the sagitta is curved laterally and the posterior end is relatively flat. The rostrum is longer than the antirostrum, but the difference increases with fish size. Prominent grooves and ridges are present on the lateral side of the sagittae and are nearly absent on the medial side (Fig. 1). The asteriscus and lapillus were much smaller and more fragile than the sagittae and have no annuluslike external or internal growth features. The small size and fragility of these smaller otoliths, as well as the time and care required to remove them, precluded additional sampling.

Greater amberjack sagittae weights ranged from 1.4 to 68.6 mg. The mean weight of male sagittae (23.2 mg) was not significantly different from that of females (25.0 mg). The relationship between FL and sagittal weight (SW) was best described with a negative exponential (following the von Bertalanffy equation). Because there was no difference in this relation between males and females ($P > \chi^2 > 0.05$) the data were combined to produce the equation (Fig. 2)

$$FL_{SW} = 151 (1 - e^{(-0.04(SW + 1.6))}),$$
 $(r^2=0.96)$

¹ Thompson, B. A., C. A. Wilson, J. H. Render, M. Beasley, and C. Cauthron. 1992. Age, growth, and reproductive biology of greater amberjack and cobia from Louisiana waters. Final report to U.S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program, NMFS, St. Petersburg, FL, NA90AA-H-MF722, 77 p.

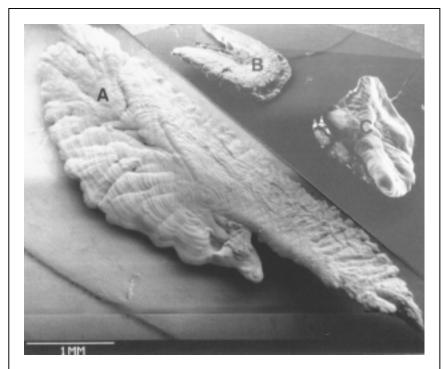
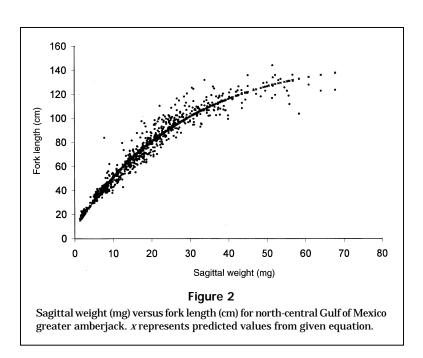


Figure 1 Scanning electron micrograph of a sagitta (lateral view) (\mathbf{A}), lapillus (\mathbf{B}), and asteriscus (\mathbf{C}) from a 42.7-cm greater amberjack from the north-central Gulf of Mexico.

where FL_{SW} = fork length (cm); and SW = sagittal weight (mg).

Although internal annuluslike features were visible in whole otoliths, they were not sufficiently translucent to permit consistent enumeration. Readability was not improved by immersing sagittae in either glycerin or clove oil for up to one year. Surface grooves and ridges were prominent on the lateral side of sagittae from young fish but became compressed and indistinguishable in older specimens owing to an over-burden of calcium carbonate; a similar observation was reported for marlin (Wilson et al., 1991). External ridges were closely associated with internal microstructure that we interpreted as annuli. Although a first and second annulus was visible in whole sagittae, we concluded that annuli could not be enumerated from whole otoliths for most fish, particularly larger specimens.

Microstructural growth features were readily visible in most sectioned sagittae; however, the only consistent annuluslike features were regions where



growth bands converged on the lateral side of the otolith section. These "convergence zones" were internal to the lateral surface of the antirostrum, where numerous growth features (increments) converged

on a common point (Fig. 3A); these features were usually associated with ridges on the lateral side of the sagitta or associated with alternating opaque and translucent zones, or with both ridges and zones (Fig. 3B). Similar structures were described and used to age istiophorids by Prince et al. (1986) and Wilson et al. (1991).

Six of 48 oxytetracycline-injected fish were recovered from the tag-recapture experiment. Oxytetracycline marks were observed in sectioned sagittae from all six fish (Fig. 4). The location of the oxytetracycline mark in relation to presumed annuli supported the use of the growth features described above.

The specimen in Figure 4 was captured in September and recaptured in March and had an annulus consisting of a ridge and convergence zone between the tetracycline mark and the margin. The combined information obtained from six oxytetracycline-marked otoliths confirmed that one annulus is formed between November and March in the sagittae of two-and three-year-old greater amberjack.

Age structure

Five hundred and ninety seven greater amberjack sagittae were sectioned and aged by two readers.

Forty-five specimens were considered unreadable owing to poor sample preparation. Pairwise comparisons between two readers indicated that 9.6% of the counts differed by 1 year, 1.6% differed by 2 years, and 0.4% differed by more than 2 years. Readers combined had a coefficient of variation (CV) of 0.15 and an index of precision (D) of 0.11.

Age estimates of greater amberjack ranged from young-of-theyear to 15 years. Mean age of males (2.9 yr) was not significantly different than that of females (3.2 yr) (ANOVA *P>F*=0.064); however, all fish over 9 years of age were female. Most of the greater amberjack sampled were from one to three years old (Fig. 5).

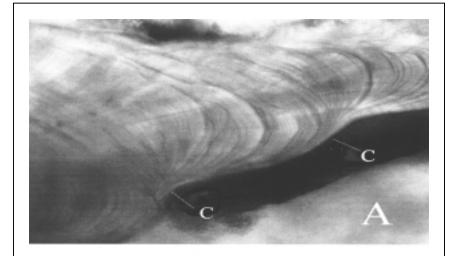
A linear function best described the relation between estimated age and sagittal weight. The regression parameters were not significantly different (ANCOVA) between males and females; therefore data were pooled and produced the relation

$$Age = 0.15(SW) - 0.44, \quad (r^2 = 0.75)$$

where SW =sagittal weight (mg); and

Age = amberjack age in years.

Growth was modeled by using the von Bertalanffy growth model (Fig. 6) to facilitate comparisons with other values reported in the literature. Our age data from



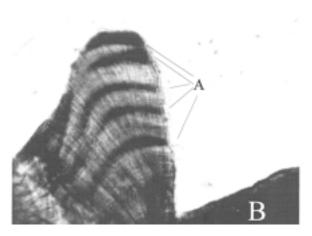


Figure 3

Photomicrographs of sectioned sagittae from a 72-cm-FL ($\bf A$) and 42-cm-FL ($\bf B$) north-central Gulf of Mexico greater amberjack. Photomicrograph A shows the convergence zones (C) along the dorsolateral edge of the rostrum. Photomicrograph B shows the opaque and translucent zones in the rostrum; opaque zones were interpreted as annuli ($\bf A$).

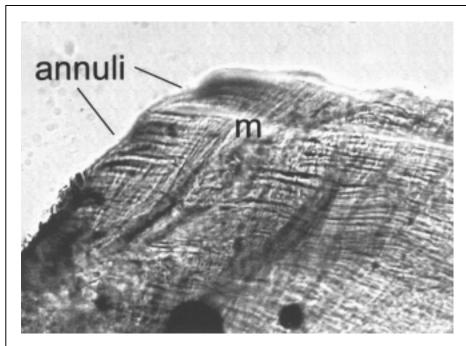


Figure 4

Photomicrograph of a sectioned sagitta from a 53-cm tagged and recaptured north-central Gulf of Mexico greater amberjack observed under ultraviolet light. The fish was at large for 160 days. Tetracycline mark = m; annuli are indicated by the arrows.

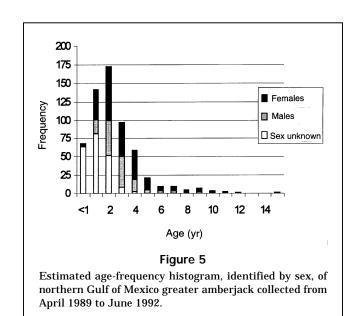
greater amberjack were fitted to the von Bertalanffy growth model (Fig. 7). Because there was no difference between male and female models ($P>\chi^2=0.496$), data were combined and resulted in

$$L_t = 138.9(1 - e^{-0.25(t + 0.79)}).$$
 $(r^2 = 0.96, n = 552)$

Tag-recapture data obtained from the CGTP yielded 25 data points useful for comparison of growth rates, and an additional six data points from our mark-recapture experiment. Predicted lengths fell along the trajectory of a line where predicted lengths equalled observed lengths (Fig. 7). The differences between observed and predicted values were both positive and negative. There was a tendency to under-predict fish size above 80 cm recapture length. The growth of tagged and recaptured fish provided additional support of our age estimation technique.



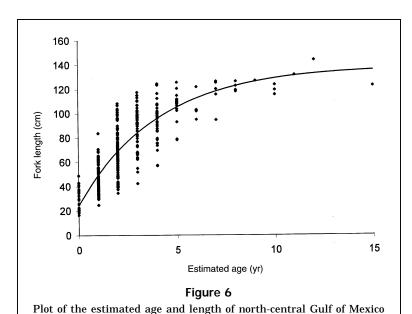
Our observations of sex-related differences in maximum size of greater amberjack are consistent with the findings of previous investigators. Burch (1979) reported a maximum size of 145.0 cm for males and of 155.5 cm for females and noted that the mean fork



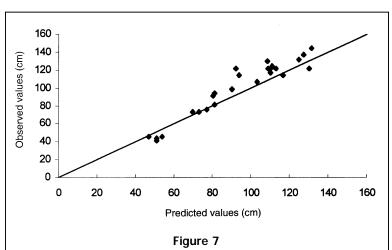
length of females was greater than that of males of the same age. Humphreys (1986) reported a maximum size of 106.0 cm for males and of 149.4 cm for females. We found that the maximum size of males (132.7 cm) was less than that of females (144.1 cm) and that females represented 72% of the fish over

100 cm. Our data support the hypotheses that the maximum size in greater amberjack is sex related. Similar results were reported for other pelagic species (Atlantic and Pacific blue marlin, and swordfish) suggesting that females either grow faster, live longer, or both (Wilson, 1984; Wilson et al., 1991).

Charterboat-caught greater amberjack were collected year-round from the Louisiana coast, providing us with the opportunities to examine seasonal changes in the population. Size-frequency analysis of these data showed that fish were largest from May to September and smallest from November to Feb-



greater amberjack and the resultant von Bertalanffy relationship.



Predicted versus observed recapture lengths of tagged greater amberjack. Predicted values were calculated by using our von Bertalanffy growth parameters. The solid line covers points where the predicted and observed values are equal.

ruary, suggesting a seasonal shift in the size frequency of individuals in the population off Louisiana. Although this seasonal size difference could be due to sampling bias, we believe that greater amberjack have an affinity for warmer waters and that the cooler waters associated with winter initiate an emigration from Louisiana waters. Burch (1979) reported greater amberjack migrating southward from December to May and northward from June to December in Florida. Baxter (1960) reported a northward migration of California yellowtail (as *Seriola dorsalis*) off California waters during early spring. The size

at which greater amberjack begin to migrate is not known (Burch, 1979).

Females tended to be more abundant than males throughout our study, although the female-to-male ratio varied with time of year and source. This is contrary to Burch (1979) who reported female-to-male ratios from 0.6:1 to 2:1 with males more numerous in all months except July, August, and September. Humphreys (1986) reported a female-to-male ratio of 0.9:1. In our study, no trend in sex ratio was detected for charterboat-caught greater amberjack, and the overall ratio was 2.5:1. It is possible that males are more abundant off the west coast of Florida and females are more abundant off Louisiana. Thompson et al.1 found that male cobia (Rachycentron canadum) dominated in the westcentral Gulf of Mexico, whereas females dominated in the east-central Gulf of Mexico.

Otoliths

Greater amberjack otoliths are small, fragile, and complex in shape. In a comparison of external and internal features with those of other pelagic species, sagittae were found to be similar in shape to those of red steenbras (*Petrus rupestris*) (Smale and Punt, 1991), tunas (C.A. Wilson, unpubl. data), billfishes (Wilson et al., 1991), and several other carangids (*Alectis, Caranx, Chloroscommbrus, Elegatis*, and *Uraspis*, senior author, unpubl. data)

We tried several models (power function, logistic equation, Gompertz and Richards models) to describe the relationship between fish size (fork length) and otolith size (sagittal weight). A negative exponential in the form of the von Bertalanffy equation provided the best fit (r^2 =0.96) and indicated that sagittal weight continues to

increase even after increases in fish length or weight slows or ceases (Pawson, 1990). This finding provides further evidence that otolith growth is more closely associated with time than with fish size as the fish becomes older. Secor and Dean (1989) suggested that otolith growth was a function of both somatic growth and time in young fish. We propose that as fish grow and approach an asymptotic size, otolith growth continues at a basal level and does not reach an asymptote. This is further evidence of the disassociation of otolith growth and fish growth in older fish. Continued sagittal growth throughout the life of the fish is the property that makes sagittae a useful ageing tool (Gamboa, 1991; Casselman, 1990).

Opaque zones (annuli) observed in transverse sections of greater amberjack sagittae were not as consistent as those reported in other species such as the sciaenids (Beckman, 1989; Casselman, 1990). Wilson et al. (1991) found that establishment of annual patterns in transverse sections of sagittae from pelagic fishes was best accomplished through interpretation of a combination of growth features on the surface of and in sectioned sagittae. Transverse sections of greater amberjack sagittae contained growth features described by Smale and Punt (1991) for red steenbras and by Wilson (1984) and Prince et al. (1986) for billfishes. We used similar criteria for discrimination of annual patterns in transverse sections of greater amberjack sagittae. Our criteria included external ridges on the lateral side of the sagittae, ridges within the sulcus acousticus, internal opaque and translucent zones, and the association of these features with a common area where many growth bands converged (Fig. 3A). All these growth features were coincident with annuli that were validated by using oxytetracycline-injected fish (Fig. 4). Smale and Punt (1991) found similar patterns in transverse sections of sagittae from red steenbras (*Petrus* rupestris). Although they reported fish as old as 25 years, transverse sections of sagittae from red steenbras looked similar to those of greater amberjack.

Disagreement over age estimates based on the above criteria was usually over an assignment of the first annulus. In some specimens a prominent opaque zone occurred adjacent to the core; we concluded it was laid down during the first winter and therefore did not consider it an annulus. Baxter (1960) reported that the first annulus was formed on the scales of yellowtail (as *Seriola dorsalis*) during their second winter, which was 18 months after hatching. We considered the first annulus in amberjack to be that which was laid down in the second year, when fish were actually 15 to 21 months old. When corrected for the discrepancy of the first annulus, the coefficient of variation and index of precision for the two

readers were 0.15 and 0.11, indicating reasonable consistency in annulus interpretation. Similar values were reported by Wilson et al. (1991) for Atlantic blue marlin.

Apparently the sex-related size difference in amberjack is due to age-related differential mortality. Most of the greater amberjack collected were under 5 years old, although we found fish as old as 15 years. Males ranged from 1 to 9 and females ranged from 1 to 15 years. Females represented 76% of the samples above age 7. Burch (1979) found female greater amberjack to age 10 and males to age 8 for fish taken by southern Florida charterboat fishermen. The only other pelagic predator that demonstrates age-related sexual dimorphism, where females outlive males, is swordfish (Wilson and Dean, 1983). Greater amberjack also share a life history similar to both great barracuda and cobia in that they are all moderately long-lived pelagic reef species, and greater amberjack could be expected to exhibit similar patterns of longevity for males and females. However, deSylva (1963) found no age difference between sexes for great barracuda (Sphyraena barracuda). Richards (1967) reported no sex-related age differences for cobia (Rachycentron canadum) from mid-Atlantic waters, and Thompson et al. 1 reported similar findings for cobia from the Gulf of Mexico. We conclude that greater amberjack males die at a younger age than do females. More research is needed to determine whether these differences are real or are the result of sampling biases used in our study.

The relation between sagittal weight and age demonstrated that otolith weight can be used to estimate relative age. This finding is consistent with that for other pelagic species (Wilson, 1984; Wilson et al., 1991). Sagittal weight can provide a useful management tool because the random sampling and weighing of greater amberjack sagittae can be used to estimate age without the additional time and cost required for sectioning. We used a negative exponential to model the relationship between otolith size and fish size. The fit of this model indicates that otolith size continues to increase over time.

Growth

The von Bertalanffy growth parameter estimates obtained in our study were similar to both Burch's (1979) and Humphreys' (1986). Like Humphreys (1986), we did not find differences by sex. Burch (1979) reported L_{∞} of 146.3 cm, 159.7 cm, and 164.3 cm for males, females, and sexes combined for charterboat- caught greater amberjack in Florida waters. Humphreys (1986) reported L_{∞} of 149.3 for Hawaiian greater amberjack (sexes combined). We

obtained an L_{∞} of 138.8 cm, slightly smaller than that obtained by other authors; differences may be due to duration of the growing season, because greater amberjack studied by other authors came from warmer climates where growth may have been more rapid. Our comparison of observed recapture lengths with predicted recapture lengths (Fig. 7) further verified our age-estimation technique. Of interest was our observation that this method tended to underestimate fish size at sizes larger than 80 cm. Because most of the tagged fish were collected off south Florida, it is possible that they grow slightly faster than those off Louisiana.

Conclusion

Our analysis provides evidence that greater amberjack from the north-central Gulf of Mexico are moderately long-lived, living up to 15 years. They demonstrate a sexual dimorphism, where females grow larger than males, but this appears to be age related because males die younger. Our use of sagittal annuli is validated for only two- and three-year-old fish and future studies will be needed to complete age validation.

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